NOTE ON THE RIGIDITY OF THE PECTORAL FIN OF *MAKAIRA INDICA* (CUVIER)*

By

Mary-Louise Wapenaar & Frank Hamilton Talbot

South African Museum

(With 1 plate and 7 figures in the text)

Abstract

It has been known for a long time that the pectoral fin of the black marlin, *Makaira indica*, cannot be folded flat against the side of the body as it can in all other istiophorid fishes. The anatomy of the pectoral girdle of the black marlin is here compared with that of the striped marlin, *M. audax*, to determine the mechanism of the rigid joint. The osteology and musculature of the pectoral girdle of both species is described and discussed, with particular reference to the articular region. It is concluded that the bony structure of the joint and the strength and disposition of its fibrous connective tissue sheath together ensure the rigidity of the pectoral fin in *M. indica*. It is suggested that the rigid pectoral fin of *M. indica* is used as a plane of elevation.

I. Introduction

Ever since Nakamura (1938) and, more particularly, Gregory & Conrad (1939) showed that the black marlin *Makaira indica* (Cuvier) has a rigid pectoral fin which cannot be folded flat against the body, while all other istiophorids have a folding pectoral fin, the reason for such a difference, and the structural features that prevent the fin from folding in the black marlin, have been a source of speculation among ichthyologists.

The pectoral fin of marlins is in the main an inflexible, sickle-shaped structure with a narrow leading edge formed by the sharp edge of the strong marginal ray, and a small movable posterior lobe formed by the last ten rays or actinosts. In all marlins it is set at an angle of about 35° to the horizontal, so that when extended at right angles to the body it acts as a plane of elevation by presenting a horizontal or oblique surface to the direction of flow of the water rather than a vertical surface as in many teleosts. In all istiophorids other than *M. indica* the fin can be rotated from the extended position to lie flat against the side of the body, but in *M. indica* the fin is permanently extended and cannot be folded against the body without structural damage, for which considerable force must be used.

An anatomical study was undertaken in which the pectoral girdle of *M. indica* was compared with that of the striped marlin, *M. audax* (Philippi), to

* This paper formed part of the Oceanography Symposium held during the 61st Annual Congress of the South African Association for the Advancement of Science at Durban, July 1963. The association has kindly given permission for publication here.

Ann. S. Afr. Mus. **48** (6), 1964, 167–180, pl. II., 7 figs.

determine the reason for the rigidity of the pectoral fin in *M. indica*. The articular regions of the pectoral girdles of *M. albida* (Poey) and *M. nigricans* (Lacépède) were also examined.

Nakamura (1938), Gregory & Conrad (1939), LaMonte & Marcy (1941), LaMonte (1955), J. L. B. Smith (1956), Robins (1957), Robins & de Sylva (1961), and Talbot & Penrith (1962) and others have referred to the rigidity of the pectoral fin of *M. indica*, but only one attempt to investigate this feature on an anatomical basis has been made (Morrow, 1957).

Morrow states that the rigidity of the fin in *M. indica* is due to three bony pads associated with the articular surface of the marginal ray of the fin, giving it a rigid three-point suspension and thus preventing it from being rotated and folded back as occurs in the other species. In our opinion this explanation is untenable, for reasons which are given below.

II. Material

Makaira indica (Cuvier)

(*a*) Two loose girdles, fresh, of a 600 lb. fish, length 2,935 mm., taken aboard the fishing vessel *Karimona* by longline west of Slangkop, Cape Peninsula, 30/1/1962. S.A.M. Reg. No. 23194.

(*b*) Anterior half, fresh, of an 800 lb. fish, length 3,210 mm., taken aboard the fishing vessel *Walvis Pioneer* by longline 40 miles west of Cape Point, 28/1/1962. S.A.M. Reg. No. 23193.

(*c*) Anterior half, fresh, of a 462 lb. fish, length 2,540 mm., taken on rod and line 25 miles west-north-west of Cape Point, 25/2/1962. S.A.M. Reg. No. 23244.

(*d*) Prepared girdle of a 1,028 lb. fish taken by longline south-west of Hout Bay, March 1961. S.A.M. Reg. No. 23054.

Makaira audax (Philippi)

(*a*) Anterior half, fresh, of a 130 lb. fish, length 2,120 mm., taken aboard the fishing vessel *Overberg* by longline west of Cape Point, 2/2/1962. S.A.M. Reg. No. 23197.

(*b*) Prepared girdle of small specimen taken west of Hout Bay by longline, March 1961. S.A.M. Reg. No. 23052.

Makaira nigricans (Lacépède)

(*a*) Prepared girdle of large specimen taken aboard the fishing vessel *Cape Point* by longline 45 miles north-west of Dassen Island, 29/6/1961. S.A.M. Reg. No. 23104.

Makaira albida (Poey)

(*a*) Prepared girdle of specimen taken by longline south-west of Hout Bay, March 1961. S.A.M. Reg. No. 23053.

III. Osteology of the pectoral girdle of *M. audax* and *M. indica*

The pectoral girdle of marlins (figs. 1, 2) is suspended from the skull by a three-pronged post-temporal and a long, flat supra-cleithrum, and is typical in consisting of a complex of three bones. There is an anterior cleithrum which has medial and lateral flanges or arms, a rod-like ventral process which meets that of the opposite side in the mid-ventral line, and two dorsal processes, an anterior, rod-like one and a posterior expanded process. The posterior bone of the complex is the coracoid, which is roughly triangular. From its antero-dorsal corner a ridge runs ventro-caudally. Above the ridge is the dorsal process of the coracoid; the ventral process of the coracoid meets the cleithrum just above the ventral process of that bone. Dorso-medially between the cleithrum and the coracoid lies the scapula, a fairly small semicircular bone perforated by the scapular foramen, through which the nerves supplying the abductor musculature of the fin pass. The scapula bears the articular surfaces for the pectoral fin.

No bony pads such as those described by Morrow (1957) were found in any of the South African specimens of *M. indica*. If they are not present in all specimens it seems unlikely that those found by Morrow are of any significance in the mechanism of the rigid joint.

The pectoral complex is very similar in *M. indica* and *M. audax*, with a major difference in the articulation of the fin (described below in section V),

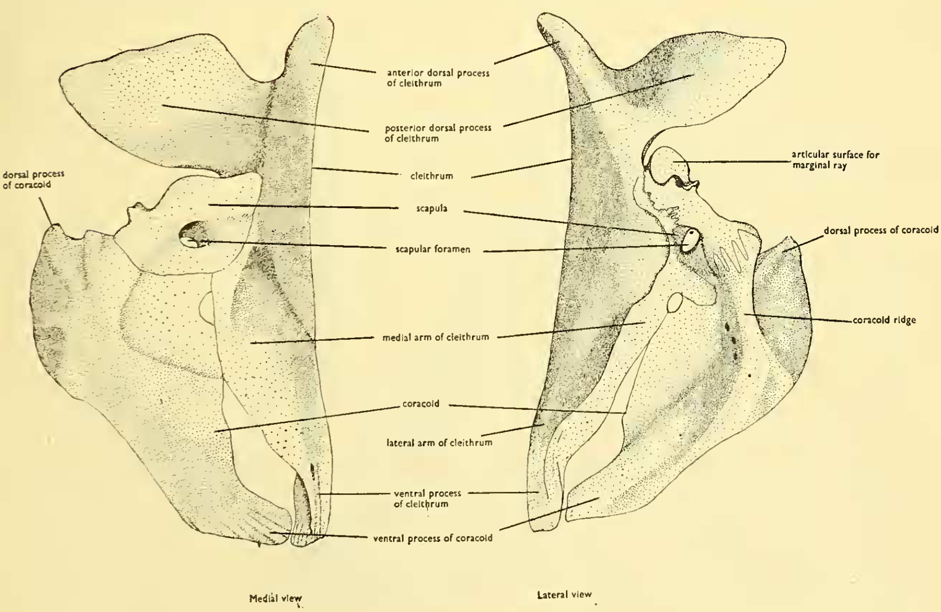

Fig. 1. Pectoral girdle of *Makaira indica*.

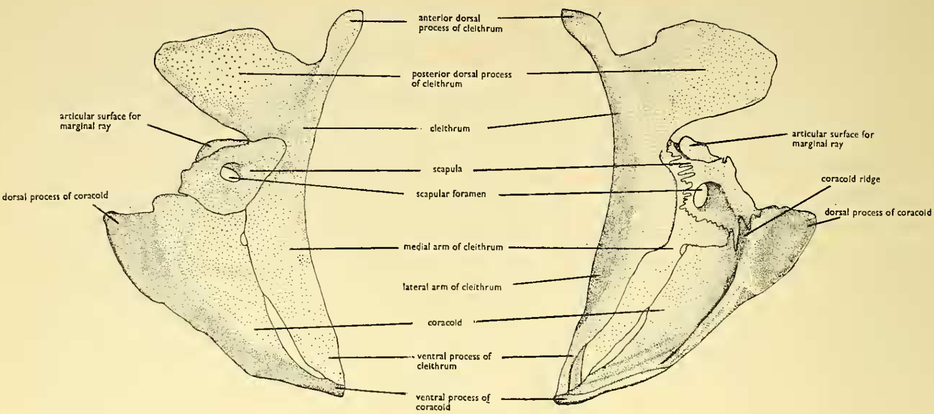

Fig. 2. Pectoral girdle of *Makaira audax*.

and other minor differences. In *M. audax* the anterior edge of the cleithrum is concave, while in *M. indica* this edge is almost straight, with the ventral process of the cleithrum somewhat backwardly directed. The coracoid ridge is shorter and heavier in *M. indica* than in *M. audax*, and the dorsal process of the coracoid is pointed in the former and rounded in the latter. The scapular foramen is relatively larger in *M. audax* than in *M. indica*.

IV. Musculature of the pectoral girdle of *M. indica* and *M. audax* (figs. 3, 4, 5)

The musculature of the pectoral girdle of *M. indica* and *M. audax* was investigated. The body muscles and the muscles between the pectoral girdle and the head and visceral skeleton were found to be identical in *M. indica* and *M. audax* and will not be included here.

The musculature of the pectoral girdle consists as in all fishes of adductor and abductor portions (Shann, 1919), which draw the fin towards and away from the body respectively. Both portions are more or less divided into superficial and deep parts, although these are often not easily separable. The abductor musculature arises from the lateral surface of the scapula and the coracoid, and the lateral surface of the medial flange of the cleithrum, and inserts on the marginal ray and the bases of the remaining rays of the fin. For most of their length from their fleshy origin the superficial and deep fibres are not clearly separable, but towards their insertion they become more distinct and have a separate tendinous insertion on the bases of the rays, the deep fibres inserting on the ventral extremities of the bases of the rays while the superficial fibres insert on a slight ridge a short distance above the bases of the rays. The last ten rays are movable in relation to the rest of the fin and have a fairly specialized musculature, some of which inserts on the radials supporting them (described below, section V). The adductor musculature arises from the medial surface

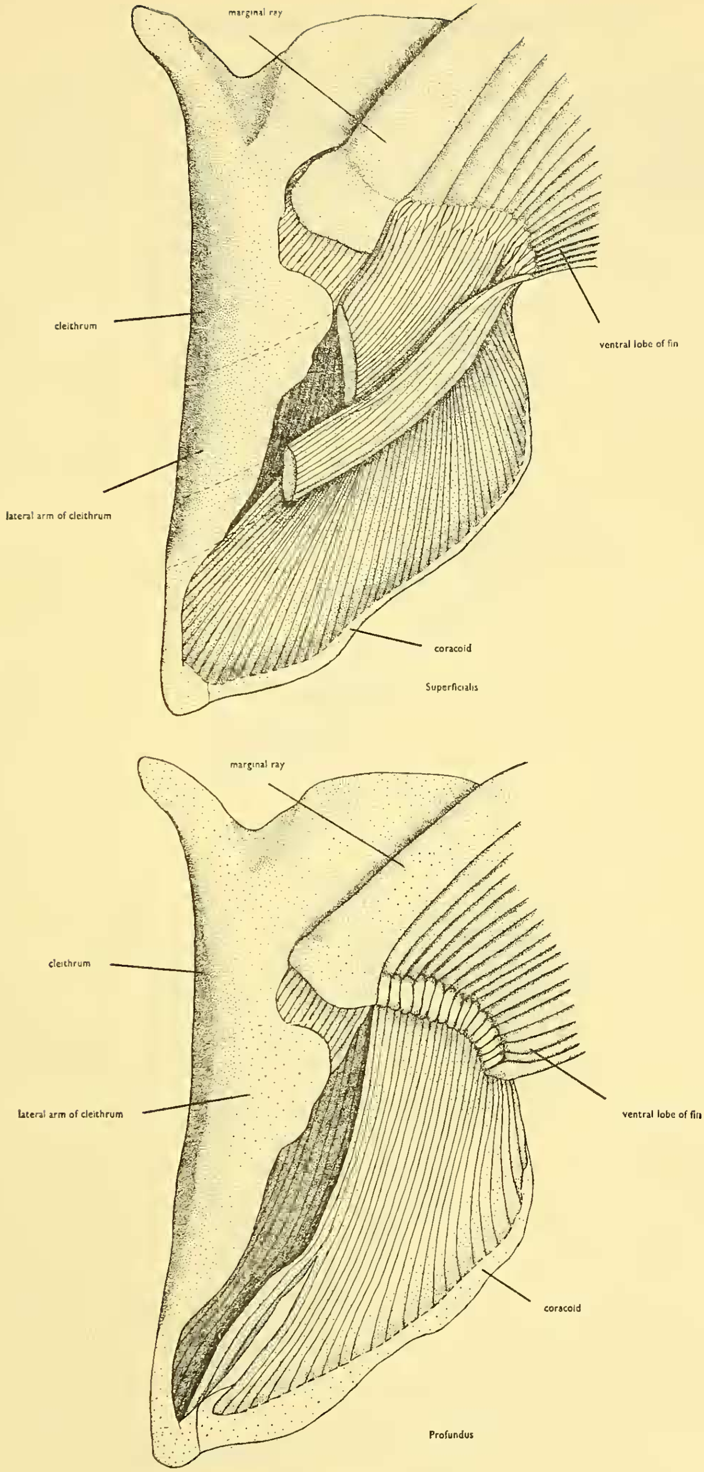

FIG. 3. Abductor musculature of *Makaira indica*.

of the cleithrum, scapula, and coracoid, and also has a tendinous insertion on the bases of the rays on the medial side of the fin. As in the case of the abductor musculature, the adductors of the last ten rays are separate and very well developed. An additional adductor, present in many fishes, the coracoradialis

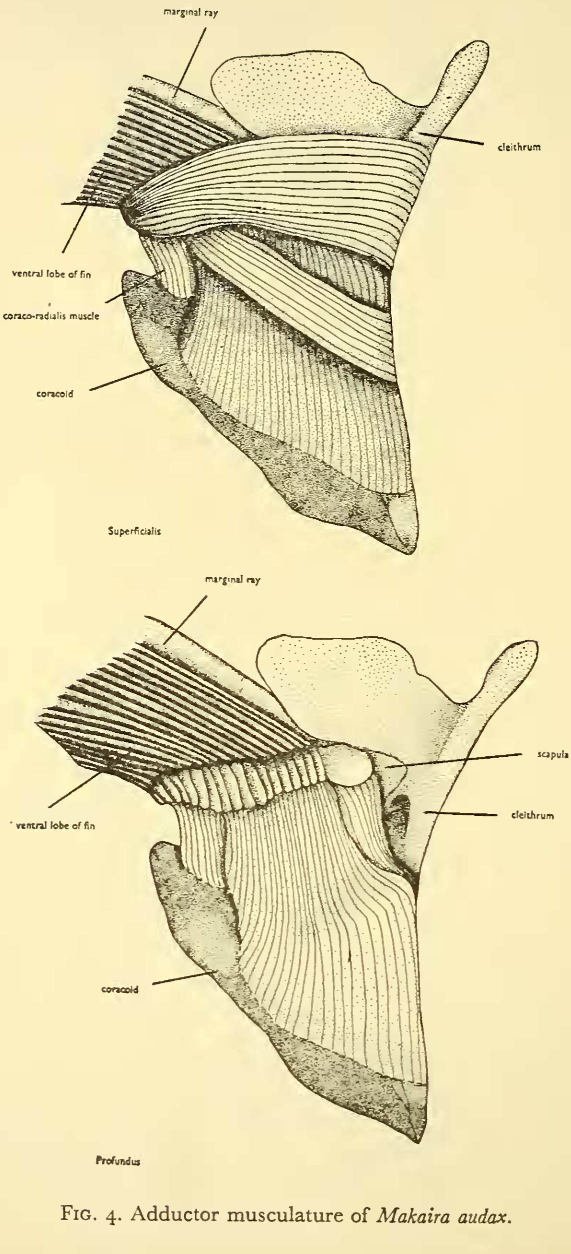

Fig. 4. Adductor musculature of *Makaira audax*.

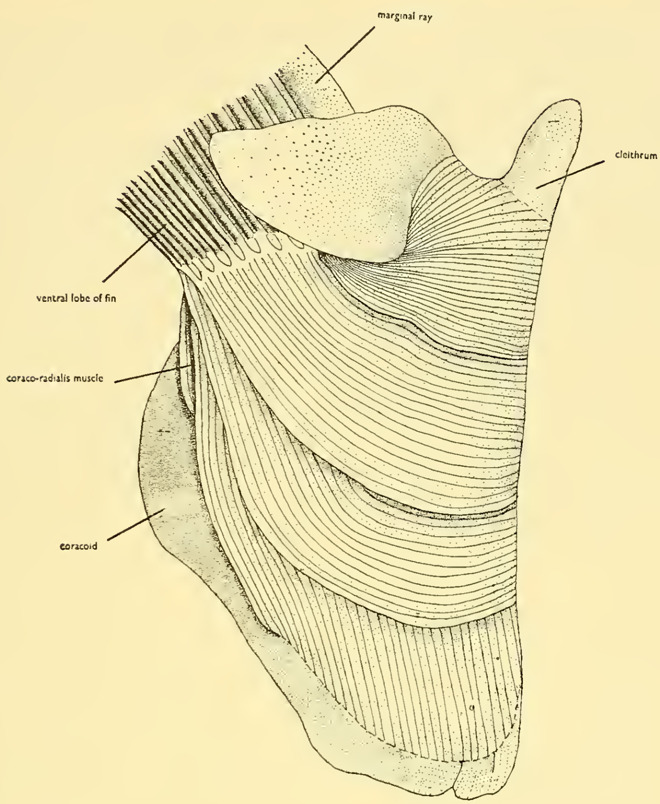

FIG. 5. Adductor superficialis musculature of *Makaira indica.*

muscle, arises from the medial surface of the coracoid and inserts on the last two radials.

In general the abductor and adductor portions are very similar in *M. indica* and *M. audax* (figs. 3, 4, 5). In *M. indica* the superficial and the deep abductor of the marginal ray form a bundle clearly separated from the abductors of the remaining fin rays, while in *M. audax* the abductors for the marginal ray are not distinct. In both species the last ten rays form a distinct lobe with a separate and well-defined musculature; the abductor portions of the musculature of this lobe are identical in the two species.

There are certain differences in the adductor musculature of the two species (figs. 4, 5); again in *M. indica* the adductors of the marginal ray are clearly defined and in addition have a slightly different origin, arising from the posterior dorsal process of the cleithrum rather than from the medial arm of the cleithrum. In general the adductor muscles in *M. audax* are arranged so that the fibres are relatively longer than in *M. indica.* The greatest difference is in the adductor musculature of the ventral lobe, with which the present discussion is not concerned as it has no bearing on the mechanism of the rigid joint. This lobe clearly has important hydrodynamic effects on the fin, however, and one would expect its mode of action to differ in two species in which the action of the fin as a whole differs strongly.

The adductor and abductor muscles then are responsible for the movements of the pectoral fin. By contraction of the abductors other than those of the ventral lobe the antero-ventral tip of the fin-base is pulled forward and downward. In *M. audax* (pl. II) this movement causes the fin to be pulled away from the body into the extended position. This actually involves two movements, the drawing downwards of the antero-ventral tip of the fin base and the drawing forwards of the fin as a whole so that the direction of the fin tip is at right angles to the direction of the body, but both movements occur simultaneously in *M. audax*. In the extended position in *M. audax* either movement can be carried out; by twisting, the plane of the fin to the water can be altered by about 10°, and the leading edge can move through any arc between the fully extended position and the folded position.

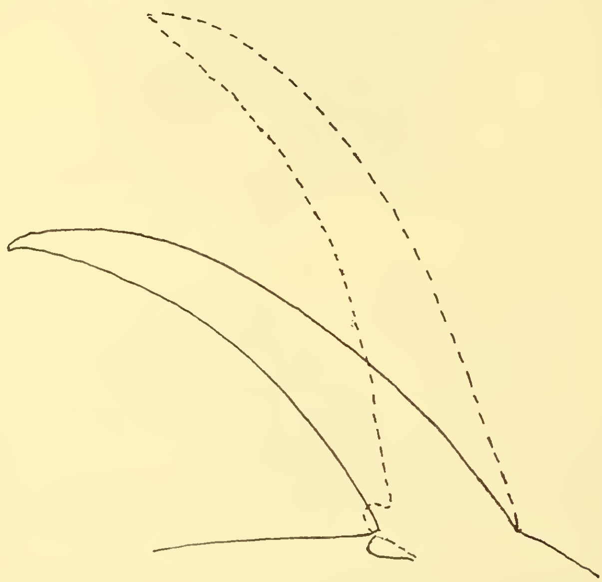

Fig. 6. Range of movement of fin in *Makaira indica*.

In *M. indica* (fig. 6), where the fin is permanently extended, two limited movements are possible, and are also brought about by the abductor and adductor muscles. The angle of incidence of the fin plane to the water can be altered within an arc of about 4°, brought about by the pulling down by the abductors of the antero-ventral tip of the marginal ray base; the fin is also capable of an antero-posterior movement in a horizontal plane through an angle of 12°. It can thus be seen that the range of movement is far more limited in *M. indica* than in *M. audax*.

It would be anatomically unusual if the rigidity of the fin were dependent on the musculature. This would imply continual sustained muscle activity to hold the fin rigid during forward movement of the fish; that is, during most of its life. The total extension of a muscle group is never limited by its own action alone (Professor L. H. Wells, personal communication). The maximum extension is normally limited by the structure (ligament, cartilage and bone) of the joint itself. If they were not limited in this way, the structure of muscle fibres is such that on relaxation they could expand until damaged. If muscles held the fin rigid in the black marlin it would also follow that in a freshly dead specimen the fin should be able to move back against the body, even if the muscle fibres were damaged in so doing. This is not the case. As would be expected, therefore, the structure of the joint itself and not the muscles is the limiting factor to further backward movement. In any joint the arrangement of the muscles will depend on the amount of movement allowed by the arrangement of the bones and ligaments of the joint. Thus in *M. audax*, where the range of possible movement of the fin is more extensive, the muscle fibres are longer than in *M. indica*.

The fin musculature of *M. indica* is very well developed in spite of the small range of movement of the fin. It is suggested that while the fin of *M. audax* encounters little water resistance in the initial stages of its extension, water pressures render considerable muscular effort necessary for moving the fin when it is extended. It is these latter movements with which the muscles of *M. indica* are concerned, so that they must be well developed, as well developed as in *M. audax*, in fact. Short fibres are adequate for these short-range movements, however.

The main point arising from the study of the pectoral musculature is that, if the abductors of *M. audax* are contracted, the pectoral fin can be maintained in the same position as that of *M. indica*, but in *M. indica* the fin is maintained in this position even when the abductor muscles are relaxed and the adductors contracted. The muscles do not assist in rendering the joint rigid; as would be expected, *M. indica* has developed some method of maintaining the rigid position of the fin other than by sustained muscular contraction.

V. Articulation of the pectoral fin (fig. 7)

The most significant difference in the pectoral complex lies in the arrangement and shape of the articular surfaces for the pectoral fin. In *M. audax*, *M. nigricans*, and *M. albida* the articular surface for the base of the marginal ray lies on the dorsal edge of the scapula; its surface is markedly convex and curves smoothly from the lateral to the medial surface of the bone; in other words it is saddle-shaped. The base of the marginal ray in these species is concave to correspond with its articular surface on the girdle. In *M. indica* the articular surface for the marginal ray, although close to the dorsal edge of the scapula, lies entirely on the lateral surface and is flat, so that a limited amount of sliding but no rolling movement is possible. The base of the marginal ray in this species is correspondingly flat. The dorsal edge of the scapula above the articular surface (which surface is occupied by the inner half of the saddle-shaped articular surface in *M. audax*) is here extremely rugose and pitted for the attachment of connective tissue.

In all four species there is at the posterior end of the articular surface for the marginal ray a shallow trough, which receives a downward process of the articular surface of the marginal ray base. This trough lies mainly on the dorsal edge of the scapula.

Posterior to the articular surface for the marginal ray are the articular surfaces for the radials (fig. 7). The radials are very similar in all four species. They are four in number, the first two being short and cubical, and the posterior two rather long and slender and forming the base of the posterior lobe of the fin. Their articulation lies mainly on the dorsal edge of the scapula; that of the

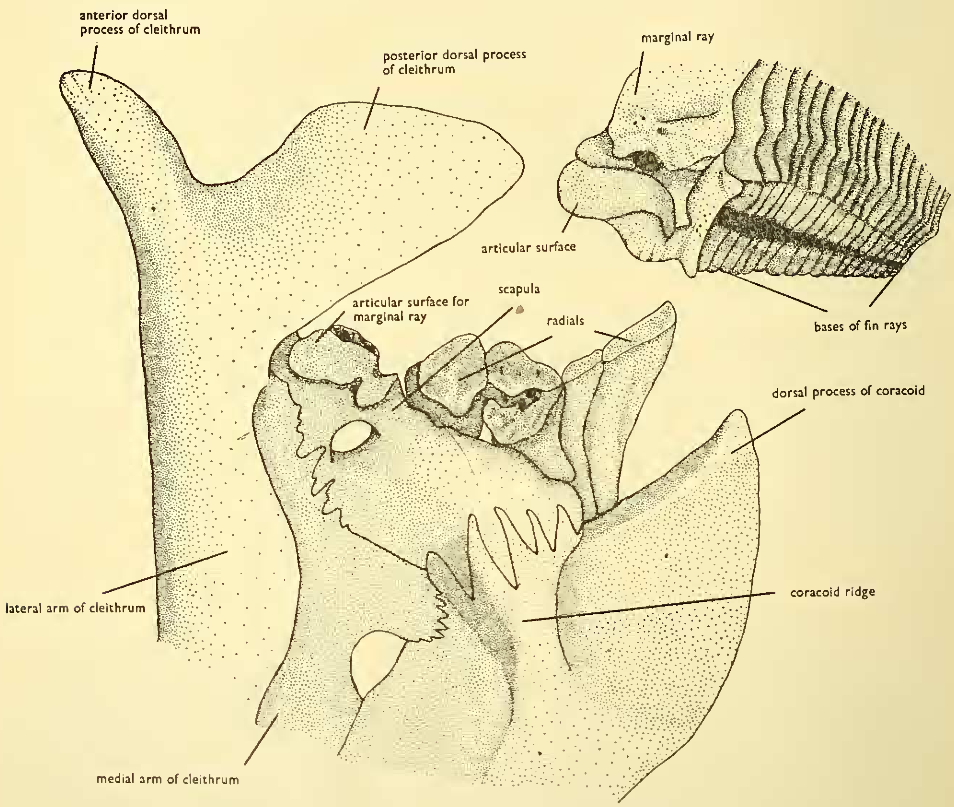

FIG. 7A. Articular region of pectoral girdle of *Makaira indica*.

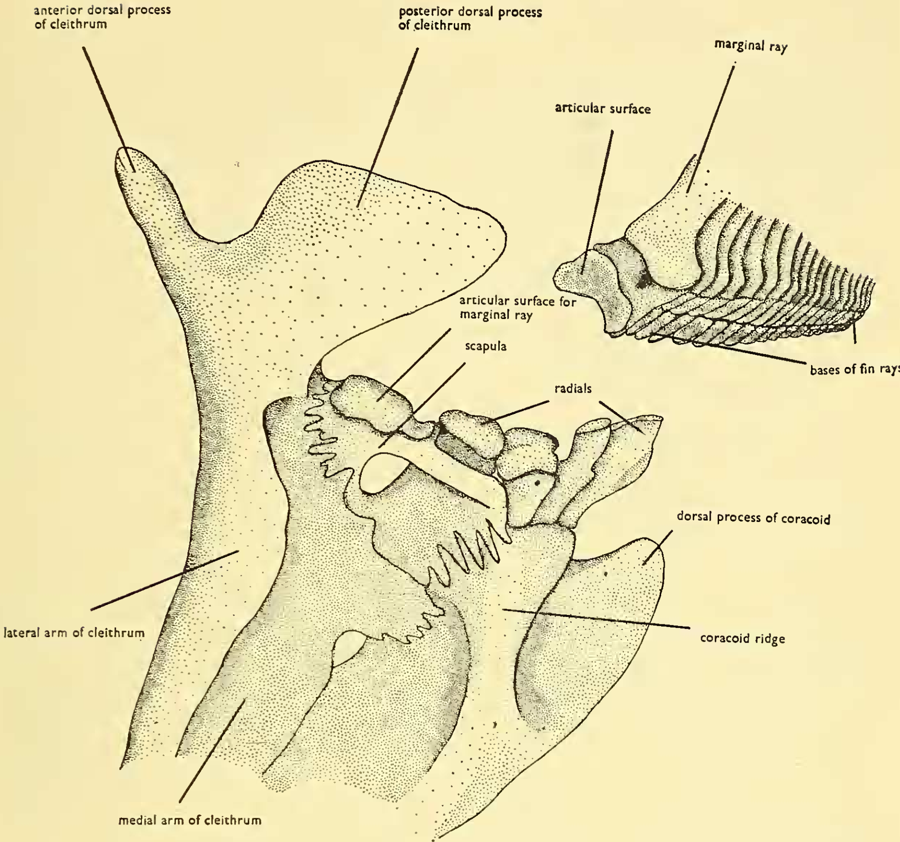

FIG. 7B. Articular region of pectoral girdle of *Makaira audax*.

first two is an area of attachment rather than articulation, most movement taking place between their distal ends and the bases of the rays. The third and fourth radials are slightly more movable, and movement is possible between the second and third radials in all species. The distal ends of the first two radials are smoothly curved in *M. audax*, allowing free movement of the rays over them, but are strongly rugose and pitted in *M. indica* for the attachment of connective tissue. The last ten rays are movably articulated on the distal ends of the third and fourth radials in both species.

In both *M. audax* and *M. indica* the pectoral fin is held to its articular surfaces by a connective tissue sheath, but this sheath shows significant differences in the two species. In *M. audax* the ligaments are elastic and loosely arranged so as to allow maximum movement of the joint, but in *M. indica* a very strong sheath of interwoven fibrous tissue is developed which holds the fin strongly to its articular surfaces; the fibres are short and their area of attachment to the bone is more extensive than in *M. audax*.

VI. Discussion

No features of the osteology of the pectoral girdle other than the articular region suggested a mechanism for maintaining the rigidity of the fin. The muscular system, although showing differences connected with the movements carried out by the fin in the two species compared, is not adapted to hold the fin away from the body in *M. indica*.

It is suggested that the only difference between the pectoral girdles in *M. indica* and the other species studied which is large enough to be of significance in the functioning of the joint of the pectoral fin lies in the position and conformation of the articular surfaces of the fin, in particular that for the marginal ray, and in the development of the connective tissue of the joint.

Owing to the flat, lateral articular surface for the marginal ray base of the fin of *M. indica*, the fin cannot roll back so that its base rests on the dorsal edge of the scapular, without leaving its articular surface; to prevent it from being forced off its articular surface by the pressures it encounters in the extended position, a very strong connective tissue sheath is developed around the joint. This tough connecting sheath prevents the fin from lying back against the body.

If the fin is forced back against the body in a dead specimen, an operation requiring considerable force, the connective tissue sheath is torn. The bones, including the radials, are undamaged, suggesting that there can be no bony locking or strutting device for maintaining the rigidity of the fin.

After the ligaments have been broken the fin can fold back considerably farther than before, but not completely as in the other species; it is stopped by the dorsal expansion of the marginal ray being jammed against the posterior edge of the posterior dorsal process of the cleithrum, which is slightly thickened in this species. Unless the ligamentous sheath is torn this position is not reached, so this is not a mechanism for holding the pectoral fin rigid.

It is suggested that at some time and for some reason in its evolutionary history *M. indica* or its ancestors found it necessary to maintain the fin in a laterally extended position. This was presumably accomplished at first by muscular contraction sustained over long periods, but in time the tension was taken by greatly strengthening the connective tissue sheath attaching the fin to the girdle, and the inner portion of the girdle's articular surface, which is used only when the fin lies against the side, was lost.

The pectoral fin of the black marlin appears to act either as a stabilizer, or as a plane of elevation. The body is very large and deep, and it may be that some stabilizing factor is necessary during forward movement. The broadbill swordfish, *Xiphias gladius*, of similar body shape, also has rigid pectoral fins. However, if this is the reason for the modification, it is surprising that the blue marlin, *Makaira nigricans*, also a large, deep-bodied marlin, does not have rigid pectoral fins.

The other possibility, that the fin acts as a plane of elevation during forward movement, deserves consideration.

It is interesting to speculate on the possible reasons for the necessity of such continuous lifting force. In pelagic surface teleosts very small marine species usually possess a well-developed closed swim bladder, but among many medium and large sized species, particularly in the Scombridae, it is variable or absent (Jones & Marshall, 1953). For example, in many species of the genus *Thunnus*, it is variably reduced or rudimentary; in *Katsuwonus pelamis*, *Sarda lineolata*, *S. chiliensis*, the genus *Auxis*, the genus *Euthynnus* and most species of the genus *Scomberomorus*, it is absent. It is probable that in fast-swimming forms which change depth rapidly a large swim bladder is a liability because of its necessarily slow change of volume. The absence or reduction of the swim bladder would necessitate some upward thrust to counteract the tendency to sink because of increased density. In such powerfully swimming fishes as the tunas and the marlins where forward movement may be continuous this presents little difficulty, and presumably the increased effort has not been too great to offset the advantage gained in vertical manoeuvrability.

Preliminary examination (dissection of one black marlin and one striped marlin) showed that the swim bladder structure is very different between the two species, and that the black marlin seems to have a relatively smaller swim bladder. This work is being continued.

It is therefore tentatively suggested that the black marlin has a reduced swim bladder, and that some upward thrust is supplied by the rigid pectoral fins.

Comparison may be made here with the sharks. In this group the pelagic surface forms are large, and in the absence of a swim bladder upward thrust is obtained by the broad and rigid pectorals.

Acknowledgements

We are indebted to the manager and skippers of the Atlantic Tuna Corporation and to Mr. F. Slack and Mr. W. Gilmore of the South African Marlin & Tuna Club for the specimens; to Dr. N. A. H. Millard of the Zoology Department of the University of Cape Town and Mr. M. J. Penrith of the South African Museum for advice and help; to Professor L. H. Wells of the Department of Anatomy, University of Cape Town, for advice on joints; and to all those who helped with the conveying and handling of the material.

The Trustees of the South African Museum gratefully acknowledge the grant-in-aid towards the cost of publishing this paper made by the Council for Scientific and Industrial Research.

References

Gregory, W. K., & Conrad, G. M. 1939. Body forms of the black marlin and the striped marlin of New Zealand and Australia. *Bull. Amer. Mus. nat. Hist.* **76**: 443–456.

Jones, F. R. H., & Marshall, N. B. 1953. The structure and functions of the teleostean swim-bladder. *Biol. Rev.* **28**: 16–83.

LaMonte, F. R. 1955. A review and revision of the marlins, genus *Makaira*. *Bull. Amer. Mus. nat. Hist.* **107**: 323–365.

LaMonte, F. R., & Marcy, D. E. 1941. Swordfish, sailfish, marlin, and spearfish. *Ichthyol. Contr. internat. Game Fish Assoc.* **1** (2): 1–24. (Not seen. Information from Morrow, 1957.)

Morrow, J. E. 1957. On the morphology of the pectoral girdle in the genus Makaira. *Bull. Bingham oceanogr. Coll.* **16** (2): 88–105.

Nakamura, H. 1938. Report of an investigation of the spear-fishes of Formosan waters. *U.S. Fish & Wildlife Serv., Spec. Sci. Rpt. Fisheries,* **153**, 1955 : 1–46.

Robins, C. R. 1957. *Charles F. Johnson Oceanic Gamefish Investigations, Progress Rpt.* 4.

Robins, C. R., & De Sylva, D. P. 1961. Description and relationships of the longbill spearfish, *Tetrapturus belone*, based on western North Atlantic specimens. *Bull. Mar. Sci. Gulf and Caribbean.* **10** (4): 383–413.

Shann, E. W. 1919. The comparative myology of the shoulder girdle and pectoral fin of fishes. *Trans. Roy. Soc. Edinb.* **52**: 531–570.

Smith, J. L. B. 1956. Swordfish, marlin and sailfish in South and East Africa. *Ichthyol. Bull.* 2, 25–33.

Talbot, F. H. & Penrith, M. J. 1962. Tunnies and marlins of South Africa. *Nature.* **193**, no. 4815: 558–559.